INTERSPECIFIC RELATIONSHIPS IN THE DROSOPHILA MULLERI GROUP

Approved:

J. J. Patterson

T. A. Painter

W. S. Stone

Edward L. Dodd 5/1/41

Homer V. Craig

R. W. Goldschmidt

J. M. Lewis

Approved:

A. P. Mogan
Dean of the Graduate School

INTERSPECIFIC RELATIONSHIPS IN THE DROSOPHILA MULLERI GROUP

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James Franklin Crow, A.B.

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PREFACE

To Prof. J. T. Patterson and Dr. Wilson Stone, whose suggestions and encouragement made this work possible, the writer gratefully acknowledges his indebtedness.

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INTRODUCTION

The genus Drosophila is particularly adapted to the study of species relationships, since its genetic and cytological possibilities are so well known, and numerous individuals from wild populations are easily available. Various population sizes and densities are represented and hence an unusual opportunity for the study of species differences is offered. Throughout the genus there are numerous subgroups with various cross-fertility relationships, indicating various levels of species differentiation.

This work was carried out in connection with a series of similar studies dealing with different groups in the genus Drosophila being done at the University of Texas. In the mulleri group there are two members, representing large dense populations, that occupy the same area, while two other members are geographically isolated from these and from each other. All are related by some degree of cross-fertility so that a study of the isolating mechanisms of these forms makes possible a better knowledge of the nature of genetic relations between species.

STOCKS USED IN THESE EXPERIMENTS

The members of the mulleri group used in this series of experiments are listed below. The group will be described fully elsewhere, so that only a brief contrasting description, sufficient for understanding the experimental results, will be given here.

1. Drosophila mulleri Sturtevant, 1921. Sturtevant's description is based on specimens collected at Houston, Texas, by Dr. H. J. Muller. This form has yellowish testes, a sharply defined abdominal pattern, and bright red eyes.

2. Drosophila aldrichi (Patterson, Ms.). This species is morphologically very similar to mulleri, but has a slightly different abdominal pattern, eyes that are more vermillion in color, and testes which turn from yellow to orange or rusty red as the fly becomes older.

3. Drosophila mojavensis* (Patterson, Ms.). This

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* In previous publications (Patterson and Crow, 1940, and Crow, 1941) arizonensis and mojavensis were considered as subspecies of D. mulleri, but at present it seems more suitable to consider them as separate species. This point will be discussed later, although the author has no intention of becoming involved in the philosophical question of the degree of difference between a species and a subspecies.

species is yellow or tan colored as contrasted to the gray color of mulleri and aldrichi. The eyes are dull red and the abdominal pattern is less sharply defined than in the other forms.

4. Drosophila arizonensis (Patterson, Ms). This species has eyes slightly darker than aldrichi but brighter than mulleri and is somewhat intermediate in color and abdominal pattern between mulleri and mojavensis.

The length of the life cycles of these species differs considerably. In mulleri the average period from the time the egg is laid until the imago emerges is 11 days under ordinary laboratory conditions (temperature 22 degrees C.). In aldrichi the time is 15-16 days, in arizonensis, 10-11 days, and in mojavensis, 12-13 days. In mulleri-aldrichi hybrids the life cycle seems to be comparable to that of the parent which takes the longer time to develop.

In the laboratory, when fed on regular banana-yeast agar, mulleri, mojavensis, and especially arizonensis breed very readily, but cultures of aldrichi are very difficult to keep going. The fact that aldrichi specimens were nearly always taken from regions where cactus was abundant suggested the use of cactus in the food, and when the fruit of the prickly-pear (Opuntia Lindheimeri) was added the stock went much better.

These species are all very similar morphologically,

although living specimens can be quite easily distinguished. It is quite doubtful, however, if these would have been classified as separate species from a study of pinned specimens. Mulleri and aldrichi are especially similar in appearance and were not recognized as distinct forms until a series of cross tests established the fact that two distinct types were present among the Texas forms. All the individuals tested have been found to belong to one or the other group.

The base stock of aldrichi is descended from a single female that had been fertilized in nature, and was trapped by Dr. J. T. Patterson near Austin, Texas, in the summer of 1938. Two stocks of mulleri have been used. The original tests were made from a stock established from a fertilized female trapped in Austin. Later a stock carrying a recessive brown eye mutant was isolated from a female captured at McAllen, Texas, in 1939. The chromosomes of the two stocks are identical as far as can be detected by salivary gland analysis. The stock of mojavensis was furnished by Prof. Warren P. Spencer who collected the original flies at Mesquite Springs, Death Valley, California. The stock may not have been derived from a single female, but has been inbred for over a year and appears to be cytologically homogeneous. The original female from which the arizonensis stock was established was trapped by Mr. Gordon

B. Mainland in Arizona in September, 1940.

In addition to the regular stocks of *aldrichi* a second strain was obtained from a female captured near Austin in 1938. This stock has brighter vermillion eyes than the other *aldrichi* stocks and differs in its cross relationships with *mulleri*. The eye color difference is due to a single recessive mutation. This stock will be referred to henceforth as *aldrichi* 2.

METHODS

In the laboratory these species were tested first in mass cultures for cross fertility relationships. It is necessary that such tests be repeated a number of times, since most of the species are very reluctant to hybridize, and in order to definitely establish the fact that two species will or will not cross requires a number of tests. One can only say that under the conditions of the experiment the cross did or did not produce hybrids. Matings were made in half pint milk bottles with 35 to 200 pairs and in shell vials with 10 to 50 pairs. Sometimes under very crowded conditions hybrids will be produced when ordinarily none would occur. In tests involving aldrichi cactus was added to the food.

For quantitative tests of degree of cross fertility pair matings were used. The matings were made in shell vials of banana yeast agar and the flies changed to fresh vials at the end of seven days. After 14 days the tubes in which both parent flies were still active were counted, and after removal of these parents, retained until the offspring had emerged and were counted.

When the parent flies were removed the female was dissected and examined for the presence of sperm in the spermotheca and ventral receptacle. Since in no case,

of several hundred examined, were offspring produced by a female in which sperm were not detected by this method, it may be assumed that the presence or absence of sperm in the female indicated whether or not successful copulation has taken place.

The problem of non-virgin females being used for matings is always present in an experiment of this kind. This was guarded against by several methods. In crosses involving mulleri females the stock carrying the recessive brown eye mutant was used. Cultures in which the female was not virgin produce brown eyed offspring and can be easily detected and discarded. Since this stock is perfectly viable and since mulleri females produce hybrids with all other species involved in the tests, the error due to the possible impairment of crossability due to the mutant seemed negligible. In other crosses the hybrids can be distinguished from the parent stocks either by appearance or by cytological analysis.

Cytological examination was made by means of acetocarmine smears.

CYTOLOGICAL RESULTS

The metaphase chromosomes of the four species are indistinguishable. Smears made from larval ganglionic tissue show that the chromosomes of these forms are all rod shaped with terminal spindle attachments. In each case the diploid set in the female consists of two long rods, eight shorter rods, and a pair of dots. In the male one of the longer rods is replaced by another of about the same length as the shorter, indicating that the longer rod is the X-chromosome.

The salivary gland chromosomes of these species are rather long but small in diameter as compared to other Drosophila. There does not seem to be as definite a chromocenter as is usually found. Often three of the autosomes along with the dot-like sixth are attached at their spindle fiber ends and the other two (the X-chromosome and one of the autosomes) are in connection with the nucleolus.

Detailed cytological data will not be given here but is being published elsewhere in connection with a chromosome map. The results of cytological analysis of the hybrids may be briefly mentioned, however.

Mulleri-aldrichi hybrids show no large chromosome rearrangements, but there is a definite tendency for the homologs to remain unsynapsed. In some cases almost a whole

chromosomes pair will fail to unite, while in others there is synapsis at various points along the length of the chromosome arms. Since these regions of lack of synapsis are not the same in different cells, they cannot be due to major rearrangements.

In mulleri-mojavensis hybrids there are a few small rearrangements and synapsis is slightly better than in mulleri-aldrichi hybrids. Salivary chromosomes from offspring of aldrichi-mojavensis crosses also show failure to pair. On the other hand, hybrids between mojavensis and arizonensis show closer synapsis than the others with several chromosome rearrangements.

TABLE I. Hybrids produced in interspecies crosses

	Mulleri ♂	Aldrichi ♂	Mojavensis ♂	Arizonensis ♂
Mulleri ♀	X	Sterile ♂ Sterile ♀	Sterile ♂ Fertile ♀	Sterile ♂ No ♀
Aldrichi ♀	None	X	No ♂ Sterile ♀	No ♂ Sterile ♀
Mojavensis ♀	None	None	X	Fertile ♂ Fertile ♀
Arizonensis ♀	None	None	Sterile ♂ Fertile ♀	X

RESULTS OF CROSSES

The qualitative results of the various possible crosses of the members of the group are shown in Table I. From this it can be seen that most of the crosses do not go reciprocally and that the fertility of the hybrids differs widely in different cases.

A more detailed account of the cross relationships between the species follows.

Mulleri female X aldrichi male. Sterile hybrids of both sexes are produced. These are similar to mulleri in eye color and abdominal pattern. The testes are very small and degenerate and the ovaries never completely develop. Very few hybrids are produced even in mass matings and the parents are very reluctant to mate.

Aldrichi female X mulleri male. This cross produced no hybrids in a large number of tests.

Mulleri female X mojavensis male. Sterile male and fertile female hybrids are produced. The appearance is somewhat more like mojavensis, especially in body color, and the males have small testes as mulleri-aldrichi hybrids. In backcrosses there is no clear segregation of colors so the difference is probably due to many factors. The females are quite fertile in backcrosses to males of the parent types and the males show considerable variation is testes size. When back-

crossed again to the same stock to which the original backcross was made, a small percentage of these males were fertile as would be expected (3% in backcross to mulleri, 8% in backcross to mojavensis, but this represents a very small sample). Location of sterility factors is complicated by the low fertility of the original cross and the lack of suitable genetic markers and crossover suppressors. However, by cytological analysis, some idea of which chromosomes must be present in fertile males may be obtained. This work is being carried out, but the results so far are inconclusive.

Mojavensis female X mulleri male. No hybrids have been obtained.

Mulleri female X arizonensis male. From numerous crosses involving about 2000 flies in mass cultures, only nine offspring were obtained. These were all males with small testes and were sterile. Although this is a small sample, there is a probability of less than one in 250 of this large a deviation from the expected one to one ratio. This, in addition to the fact that in mulleri the females emerge first and occur in larger numbers than males, makes it seem quite certain that there is some factor reducing the percentage of females.

Arizonensis female X mulleri male. No hybrids have been obtained.

Aldrichi female X arizonensis male. From numerous

crosses made with these species only one bottle showed larvae. From these one sterile female emerged. She was definitely weak in appearance and had abnormal wings.

Arizonensis female X aldrichi male. No hybrids have been obtained.

Aldrichi female X mojavensis male. From the numerous crosses made only 24 offspring have resulted. These were all females of intermediate appearance and sterile.

Mojavensis female X aldrichi male. No hybrids have been obtained.

Mojavensis female X arizonensis male. This cross goes more readily than any of the above although there is still considerable isolation. The hybrids of both sexes are fertile, both among themselves and in backcrosses. A preliminary test indicated that the male hybrids are not fertile to mulleri females, although not enough individuals were obtained to make the test conclusive. At least the hybrids do not seem to be conspicuously more fertile than their parents. The fertility in backcrosses will be shown in tabular form later.

Arizonensis female X mojavensis male. This cross produces hybrids much more readily than any other combination. The female hybrids are very fertile in backcrosses but the males are sterile. Quantitative data on this will be given later.

Recently two new stocks have been obtained and tested by Dr. J. T. Patterson. These were obtained from Argentina and Sicily, and according to genetic and cytological analysis appear to be the same species which has been named D. buzzatii (Patterson, Ms.). Preliminary tests show that the males of this species are very slightly cross fertile to mulleri and arizonensis females. With arizonensis only larvae were produced and these never went to maturity, while the mulleri-buzzatii cross produced a few larvae, one of which matured. The hybrid female was sterile and had an abnormal abdomen.

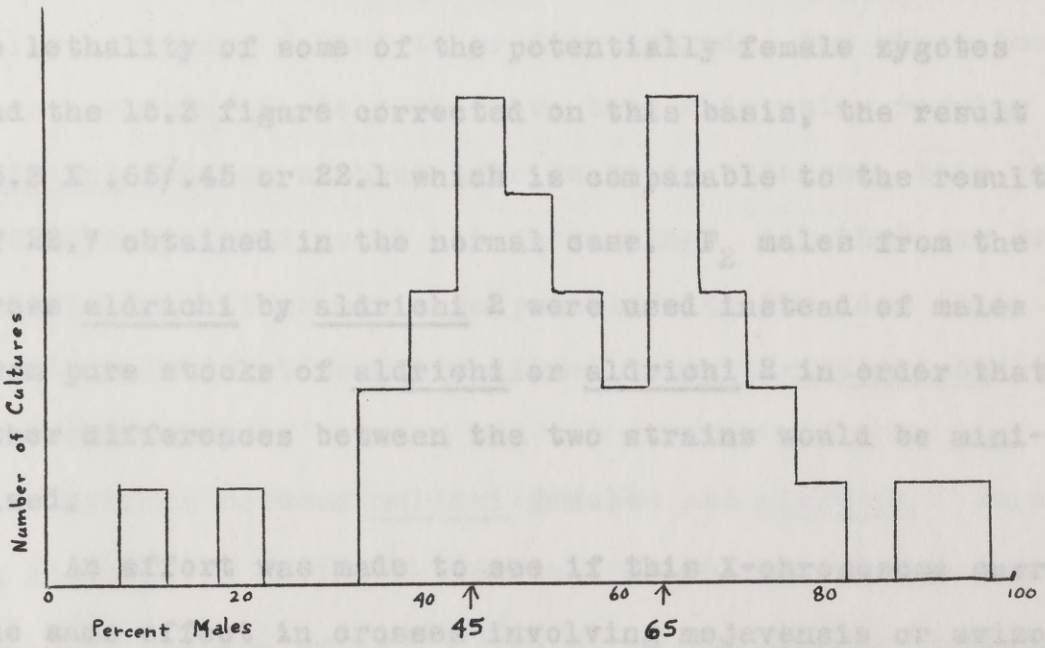
In addition to the above stocks, a strain of aldrichi (aldrichi 2) has been tested and found to differ from the other aldrichi strains in certain inter-species relations. This is identical with the others cytologically and differs phenotypically only in the possession of a recessive vermillion eye mutant.

When males of this strain are crossed to mulleri females the offspring are predominantly male and a large number of these males show an abnormal abdominal pattern similar to that of the mutant bobbed. As the cultures become more and more crowded the percentage of males increases, suggesting that the viability of the females is impaired. The females that are produced are noticeably abnormal and usually have wing deformities.

The following results were obtained from a series of crosses.

Cross	Percent males	
	Mass culture	Pair matings
aldrichi ♂ X *mulleri* ♀	46	
aldrichi 2 ♂ X *mulleri* ♀	91	
aldrichi 2 ♂ X *aldrichi* ♀		
F_1 ♂ X *mulleri* ♀	47	45
aldrichi ♂ X *aldrichi* 2 ♀		
F_1 ♂ X *mulleri* ♀	88	65

aldrichi 2 ♂ X *aldrichi* ♀
F_1 ♂ X F_1 ♀
F_2 ♂ X *mulleri* ♀ (in pair matings)



These data indicate that there is a gene, or series of genes, on the X-chromosome of aldrichi 2 which has no noticeable effect within the species but acts as a dominant semi-lethal in interspecies crosses.

That this sex ratio is due to lethality of the female zygotes and not to some sort of sex reversal mechanism seems more plausible. The following results support this.

When F_2 males from the cross aldrichi female by aldrichi 2 male are crossed to mulleri females in pair matings half the cultures show the unusual sex ratio. The average number of offspring per tube of those with the abnormal sex ratio is 15.3 while in the others it is 22.7. It will be remembered that the flies are normally about 46 percent males, but 65 percent in the stocks with the abnormal ratio. If it is assumed that the difference in sex ratio is due to lethality of some of the potentially female zygotes and the 15.3 figure corrected on this basis, the result is 15.3 X .65/.45 or 22.1 which is comparable to the result of 22.7 obtained in the normal case. F_2 males from the P_1 cross aldrichi by aldrichi 2 were used instead of males from pure stocks of aldrichi or aldrichi 2 in order that other differences between the two strains would be minimized.

An effort was made to see if this X-chromosome carries the same effect in crosses involving mojavensis or arizonen-

sis as it does with mulleri. It is known that crosses between aldrichi females and mojavensis males produce only female offspring. If the gene (or genes) acts the same way in this cross, there should be either no hybrids at all or a few weak females. In no case were offspring produced from this experiment although numerous tests were made and in some cases the females had been fertilized as evidenced by the presence of sperm in the ventral semenal receptacle. However, since crosses between aldrichi and mojavensis are so rarely obtained, these results are not absolutely conclusive, but may be taken as indicative of the fact that the same lethal effect is produced by the aldrichi 2 X-chromosome in crosses involving mojavensis as in those where mulleri is concerned.

Crosses between aldrichi 2 females and arizonensis males have also failed to produce hybrids, but since the same number of tests could have been made using regular aldrichi females without hybrids being obtained, this cannot be considered as at all convincing. All that can be said is that it is not incompatible with the idea that the lethal effect is not confined to mulleri-aldrichi 2 crosses.

Hybrids between mulleri females and aldrichi 2 males, in addition to having an abnormal sex ratio, often show an abnormal abdomen effect in the males. Whether this is an

effect produced by the gene bobbed is not known. The penetrance is low since only about 25 percent of the males show the effect clearly. In crosses between aldrichi males and mulleri females the incidence of males with abnormal abdomens is less than one percent. The percentage of abnormal males in the hybrids produced by various crosses is given below.

Cross	% abnormal males, with standard deviation
aldrichi 2 ♂ X mulleri ♀	25.3 ± 4.9
aldrichi ♂ X mulleri ♀	less than 1
aldrichi 2 ♂ X aldrichi ♀ F_1 ♂ X mulleri ♀	11.1 ± 3.6
aldrichi ♂ X aldrichi 2 ♀ F_1 ♂ X mulleri ♀	11.4 ± 2.1

The above results indicate that the gene or genes involved are not carried on the X or Y chromosome.*

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* Due to the low penetrance of the abnormal abdomen effect at high temperatures and statistical errors of sampling in the small number of cases involved, this first appeared to be acting as a gene being transmitted from father to male offspring, and this suggestion was offered (Crow, 1941). Later results do not verify this explanation however.

Table II. Percentage of Females Fertilized in Pair Matings

	Mulleri ♂	Aldrichi ♂	Mojavensis ♂	Arizonensis ♂
Mulleri ♀	84	0	5	0
Aldrichi ♀	0	88	17	0
Mojavensis ♀	0	0	96	77
Arizonensis ♀	0	0	33	90

Table II shows the quantitative results of the various crosses possible with the members of the group. The data were obtained from pair matings made as described previously. In each case the figure represents the percent of females which had been fertilized in the 14 day period.

It will be noted that some of the crosses known to produce hybrids are indicated as having produced none. That is in accordance with the expectation, when one considers the difficulty of obtaining the hybrids even in mass cultures left for long periods of time. These results are from pair matings left for only two weeks. The number of progeny and the number of females fertilized could have been increased in the crosses involving aldrichi by the addition of cactus to the food, but in order to keep the conditions as near constant as possible, all matings were made using the same food. Since the results are not completely reproducible the figures are probably not accurate within less than 10 or 15 percent. The mathematical standard deviations are much less than this and hence are omitted to prevent giving a false appearance of reliability to the data.

The degree of fertility of the hybrids between arizonensis and mojavensis is shown in the following results. These were obtained from pair matings under the same conditions as those of the original parent crosses.

Cross				% of females fertilized	% of females producing offspring
mojavensis ♀	X	*arizonensis* ♂			
F_1 ♀	X	*arizonensis* ♂		78	67
F_1 ♀	X	*mojavensis* ♂		100	100
F_1 ♂	X	*arizonensis* ♀		80	36
F_1 ♂	X	*mojavensis* ♀		56	43
arizonensis ♀	X	*mojavensis* ♂			
F_1 ♀	X	*arizonensis* ♂		89	87
F_1 ♀	X	*mojavensis* ♂		100	100
F_1 ♂	X	*arizonensis* ♀		0	0
F_1 ♂	X	*mojavensis* ♀		0	0

GEOGRAPHICAL DISTRIBUTION AND HYBRIDS IN NATURE

The exact geographical distribution of these forms is not completely known. Collection records of the two western forms are not available although Prof. Spencer states that mojavensis is very common in California deserts.

Mulleri has been found over the whole state of Texas except for the Trans-Pecos area. It is most common in the southern and central parts of the state and is rare in the wooded eastern regions. The population is known to extend some distance into Mexico and the finding of a mulleri-like form (buzzatii) in South America suggests that perhaps the population extends through Central America. Aldrichi has almost the same distribution and has recently been taken in Oklahoma.

Together these two species form the third largest Drosophila population in Texas, being exceeded by the hydei and melanogaster-simulans groups. Since these latter forms tend to follow the habitats of man it is possible that the mulleri group is the largest natural population.

There is some correlation between the presence of cactus and the size of the mulleri and aldrichi populations. Especially the aldrichi group is found in regions where cactus is present. Mulleri is often found in large numbers feeding on other food.

Of the members of this group collected, 26.1 percent have been aldrichi and the remainder mulleri. This percentage varies considerably in the different ranges of the population.

There is an interesting relationship between the proportion of aldrichi in the population and the presence of mulleri-aldrichi hybrids. The hybrid males can be detected by their small testes and have been recorded as collected. In populations containing both species, but where no hybrids were taken, the aldrichi specimens comprised 13 percent of the mulleri-aldrichi population. In populations where hybrids were found aldrichi represented 56 percent, and in one case where nine hybrid males were found in a collection of 277 male flies the population was 79 percent aldrichi. This might be expected in view of the fact that the hybrids are produced from mulleri females and aldrichi males.

DISCUSSION

In the mulleri series there are several species still in the process of becoming completely separated. The isolating mechanisms are still incompletely formed and hence may be more easily studied than in species which are more completely separated.

How effective geographical isolation is in the mulleri group cannot be answered at present. Obviously, the particular individuals of mojavensis and arizonensis obtained by this laboratory were geographically isolated from each other and from the mulleri and aldrichi of Texas, but whether the populations overlap at some point is not known. It surely must have played a part in the evolution of the differences between the Texas and Western groups.

There is a geographical separation of a sort operating in the case of mulleri and aldrichi, due to their different food preferences. Hence, even if there were no sexual isolation, there would certainly be non-random mating of the individuals of the two groups due to the fact that aldrichi tend to stay near cactus while mulleri is found on decaying fruit and vegetables.

The quantitative data clearly shows sexual isolation to be an important factor in the speciation of the mulleri group. Except in the crosses between mojavensis and

arizonensis, only a very small percent of the females were fertilized in pair matings. These crosses represent more or less forced matings since males and females of the same species were not allowed together. The results obtained in the laboratory, low as they were, probably would not be duplicated in nature where the flies had their choice of mates.

A brief test of species preference was made and showed the same results. The offspring produced when mulleri females were placed in bottles with aldrichi, mojavensis, and mulleri males were over 99.5% mulleri.

The results seem to indicate that the most effective barrier to cross breeding in the mulleri group, disregarding geographical isolation which cannot be measured at present, is sexual preference or isolation. It has often been mentioned that sexual selection is the most efficient form of isolating mechanism since reproductive effort is saved and there is no competition from hybrids.

Throughout the genus Drosophila there are numerous cases where sexual selection plays a part. Sturtevant (1920) has shown that in mixed cultures D. melanogaster and D. simulans prefer members of their own species for mating partners. Lancefield (1929) showed that the same preference is shown by the A and B races of D. pseudoobscura. In the D. virilis group there is definite sexual isolation,

both between species and between strains within a species (Patterson, Stone, and Griffen, 1940, and Stalker, 1941). In D. repleta there is sexual isolation, apparently without any other mechanisms of separation, between various strains. This may indicate that sexual isolation is the first step in species differentiation, preceeding the other forms (Wharton, 1941). Even individual mutants in D. melanogaster have been shown to have a definite preference for their own type (Spett, 1932, and Diederich, 1941).

Just how much zygotic elimination occurs in these crosses has not been effectively determined. Egg hatch counts in the mulleri group are very difficult to obtain and even in pure strains satisfactorily high control counts have not been obtained. However, in many of the hybrid crosses the number of offspring produced by females known to have been fertilized by males of another species is considerably less than the number produced by females fertilized by a male of the same species. This is particularly true in the cross mojavensis female X arizonensis male, where 77 percent of the females were fertilized but only 3 percent produced offspring, as opposed to the reciprocal cross where 33 percent were fertilized and 75 percent of these produced offspring. This indicates that there is some isolating factor or a series of factors

working between the time of insemination and the emergence of the adult offspring.

Various degrees of hybrid sterility are present, most often in the males. In three, or possibly four, of the seven cases the male hybrids are either sterile or do not occur at all. The cross between mulleri females and arizonensis may possibly belong to this category as well, if one postulates that in addition to the sterility of the males there is a gene or set of genes in the arizonensis X-chromosome that causes the same effect as in the cases involving aldrichi 2.

Haldane has stated that in hybrids the heterozygous sex is more likely to be weak, rare, or sterile than the homozygous. If each of the species has a peculiar balance between the X-chromosome and the autosomes, this balance would still be maintained in the females but would be upset in the males (Haldane, 1922). The mulleri series upholds this hypothesis. Much of the hybrid sterility may be due to genic unbalance, although a Y-autosome unbalance may be effective as well as an X-autosome relation.

Isolation of this type would seem to be built up incidental to the process of evolution of the separate genotypes rather than being caused by specific genes selected as isolating factors. That isolating factors are not selected for as such is indicated by the fact that they are

found in species geographically isolated as well as those which live in the same locality. From the point of view of variability it would be more efficient in species living together to have only one hybrid sex sterile since this would provide a method of occasional gene transfer from one species to another. Coupled with enough sexual isolation to prevent excessive competition from hybrids a mechanism of this type could theoretically produce a very satisfactory system for rapid evolution.

Exceedingly interesting is the case of aldrichi 2. Here, a species, already completely isolated from mulleri by virtue of the complete sterility of the hybrids, has acquired an additional isolating mechanism making the system more efficient. The elimination of almost half the hybrid zygotes by this lethal effect removes the competition from the hybrids themselves, hence would be of advantage to both parent populations.

No other cases of this type have been reported in animals, but a parallel case has been found in plants of the genus Crepis by Hollingshead (1930). Certain strains of C. tectorum carry a dominant gene which has no effect within the species, but in crosses with C. capillaris causes the hybrid to die in the cotyledon stage. It was found to be present in some localities and absent in others. The gene was found to be effective against C.

leontodontoides and bursifolia but not in hybrids with setosa and taraxicifolia.

Since in flies with abnormal abdomens, the sclerites are disarranged and missing, this must certainly be classed as a detrimental effect and flies of this type would probably be eliminated rapidly in competition with normal individuals in nature. Likewise the females that do survive are noticeably weak. Hence it would be unlikely that more than a very small percent of the hybrid zygotes produced by mulleri and aldrichi 2 would survive and the combination of the two effects would result in almost complete lethality when the zygote was subjected to the competition of a natural environment.

As yet only a very incomplete study of the prevalence of these factors in populations of aldrichi has been made. In addition to the individuals caught near Austin, the two genes have been found singly in specimens taken in Fayette County, Texas. Whether there is actually enough selective advantage in these effects to cause their spread in the population will make a very interesting study in light of the fact that the two species are already isolated sexually and by hybrid sterility. Whether or not this mutant (the sex ratio gene) confers enough advantage to be selected for, it still demonstrates that such mutations (acting as lethals in hybrids, but still having no effect

within the species) are occurring in Drosophila populations and could be effective under the right conditions.

As mentioned before, it seems that the mutant causing the female lethality is probably not specific for mulleri-aldrichi 2 hybrids, but is also effective in crosses involving mojavensis and arizonensis. The effect would seem to act in any environment that is not normal for it rather than acting in a specific hybrid environment.

The mulleri series illustrates a number of methods of isolation and shows very clearly that in nature the same basic results may be attained by widely different methods. That the sum of the isolating mechanisms is already effective in nature is indicated by the very small number of hybrids obtained from wild populations. Out of several thousand mulleri and aldrichi taken in Texas only 26 hybrid males were included.

The Texas populations of mulleri and aldrichi are comparatively large and dense, and all individuals tested from this area fall clearly into one or the other group. The same is true for D. hydei (Stone, unpublished). In this species all the individuals tested have been found to be perfectly fertile to each other. Contrasted to this is the case of D. virilis where three species of the red group were found among twelve flies captured (Patterson, Stone, and Griffen, 1940 and 1941). D. virilis represents a very

sparse population where genetic changes would be expected to become homozygous and thus fixed in certain localities. This would not be possible in large dense populations as pointed out by Wright (1931).

Of interest and significance is the fact that mulleri and aldrichi are closely related species living in the same environment. Volterra showed mathematically that under certain conditions two species competing for the same food supply could come to equilibrium only when one completely replaced the other (Chapman, 1931). This concept has been extended to include other factors than food by Gause (1934). Thus two species competing for the same ecological niche would come to equilibrium only when one was completely destroyed. The mathematics of this is shown in the appendix.

However, if some part of the utilization of the environment is different for the two species, there may be an equilibrium between the two where both may persist. Mulleri and aldrichi fit into this scheme very nicely. Although very similar morphologically and having arisen presumably from a common stem, they do have different feeding habits and thus occupy different ecological niches. Thus both are able to survive in the same environment because each uses a slightly different part of it.

The fact that the two species are so similar does

not necessarily mean that they are of recent origin, since the populations are dense enough to be evolving quite slowly and the environmental factors influencing the two groups are very nearly identical.

It is quite difficult to conceive of a new species splitting off in a large population. A gene causing sexual isolation, if it became homozygous in several individuals (or a dominant mutant that arose simultaneously in two or more individuals), could either be lost or replace its normal allelomorph in the population, depending on variations due to chance and selective advantage. But this would not be an efficient way of replacement of a gene in a population by a more advantageous allelomorph, since a gene that did not confer isolation would be able to spread more rapidly throughout the population. Hence such changes would probably not occur often even if such genes, i.e. conferring both isolation and selective advantage, were arising in the population.

If both the old and the new species are to survive, they must utilize at least partially different environments. It seems more logical, then, that separation of the two types was by geographical or other external means at first, and that the isolating mechanisms arose more or less incidently and spread in the populations due to their selective advantage, or due to the fact that the other changes

which they produced were of selective advantage.

Mulleri and aldrichi are most dense in the southern parts of the state and apparently have not invaded the northern and eastern parts of the United States, but the population is known to extend into Mexico. Also the two western forms are found in warm climates. It was suggested (Patterson and Crow, 1940) that perhaps the mulleri group arose as two branches from a common ancestor somewhere to the south, perhaps in Central America, and that these branches migrated along the east and west sides of the Rocky Mountain System to their present locations. Further information appears to strengthen this hypothesis.

Arizonensis has since been added to the known members of the group and, although differing from mojavensis, it is still much more closely related to that form than either are to mulleri or aldrichi. It is conceivable that two branches arose and that, at a later period, the western group split into arizonensis and mojavensis while the eastern part became mulleri and aldrichi.

The discovery by Patterson that D. buzzatii, from Argentina, is closely related to the North American mulleri group is very significant in this connection. It seems quite probable that there are mulleri forms between Mexico and Argentina that form a link between these two groups, and that in some regions of the Western Hemisphere

there may be the more primitive forms from which both the North and South American groups have come. If such forms exist, one would expect to find them in tropical localities. Here fly populations would be dense, large, and constant, and therefore under conditions favoring very slow evolution.

SUMMARY

1. A series of tests with four species of the Drosophila mulleri group show them to be related by some degree of cross fertility, although most of the species do not cross reciprocally.

2. In most cases the hybrids produced show some sterility, unusual sex ratios, and various abnormal somatic characters.

3. Several isolating mechanisms are present, such as geographical separation, sexual selection, genic unbalance in the hybrids, genes acting as lethals in hybrids, and hybrid sterility. The sum of these factors effectively prevents cross breeding.

4. It is postulated that the Texas and West Coast members of the group arose as branches from a common stem and that primitive forms related to both groups might be present in tropical South America.

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APPENDIX

The following mathematical calculations, taken largely from Volterra (Chapman, 1931), show that two species contending for the same food could come to equilibrium only when one completely replaced the other.

If only one species is concerned, the rate of change of the number of individuals in the population (N) will be given by

$$\frac{dN}{dt} = nN - mN = (n - m)N$$

where t denotes time, and n and m are constants denoting the percentage of the population being born and dying in the time interval dt.

Letting $(n - m) = E$,

$$\frac{dN}{dt} = EN, \text{ and upon integration,}$$

$$N = N_0 e^{Et}$$

where N_0 represents the number of individuals at time 0.

In the case of two species contending for a common food supply, the rates of increase if the food is sufficient are

$$\frac{dN_1}{dt} = E_1 N_1 \quad \text{and} \quad \frac{dN_2}{dt} = E_2 N_2$$

Suppose each species decreases the food supply which is

available to both,

N_1 decreases it by $h_1 N_1$

N_2 decreases it by $h_2 N_2$

Together they decrease the amount by $h_1 N_1 + h_2 N_2$

Then the coefficients of increase, instead of being E_1 and E_2, become

$$E_1 - C_1(h_1 N_1 + h_2 N_2) \text{ and } E_2 - C_2(h_1 N_1 + h_2 N_2)$$

and the rates of change are

$$\frac{dN_1}{dt} = \left[E_1 - C_1(h_1 N_1 + h_2 N_2)\right] N_1 \quad \text{and}$$

$$\frac{dN_2}{dt} = \left[E_2 - C_2(h_1 N_1 + h_2 N_2)\right] N_2$$

where E_1, E_2, C_1, C_2, h_1, and h_2 are constants.

Then, since $\int \frac{dN}{N} = \log N$

$$\frac{d \log N_1}{dt} = E_1 - C_1(h_1 N_1 + h_2 N_2)$$

$$\frac{d \log N_2}{dt} = E_2 - C_2(h_1 N_1 + h_2 N_2)$$

Multiplying and subtracting,

$$C_2 \frac{d \log N_1}{dt} - C_1 \frac{d \log N_2}{dt} = E_1 C_2 - E_2 C_1$$

Integrating,

$$\log \frac{N_1^{C_2}}{N_2^{C_1}} = (E_1 C_2 - E_2 C_1)t + K \quad \text{or}$$

$$\frac{N_1^{C_2}}{N_2^{C_1}} = K' e^{(E_1 C_2 - E_2 C_1)t}$$

Now, if $E_1 C_2 - E_2 C_1$ is greater than 0,

$$\lim_{t \to \infty} \frac{N_1^{C_2}}{N_2^{C_1}} = \infty$$

If $N_1 \geq \frac{E_1}{C_1 h_1}$, $\frac{dN_1}{dt}$ becomes negative.

Hence N_1 is finite, and since

$$\lim_{t \to \infty} \frac{N_1^{C_2}}{N_2^{C_1}} = \infty$$

N_2 must approach 0 as t becomes infinite.

When N_2 becomes small enough to remain negligible, the equation for the rates of change becomes

$$\frac{dN_1}{dt} = (E_1 - C_1 h_1 N_1) N_1$$

Separating the variables and integrating

$$t = -\frac{1}{E_1} \log \left(\frac{E_1 - C_1 h_1 N_1}{N_1}\right) + K'$$

$$N_1 = \frac{K E_1 e^{E_1 t}}{1 + C_1 h_1 K e^{E_1 t}} = \frac{K E_1}{e^{-E_1 t} + C_1 h_1 K}$$

and as t is large

N_1 approaches $\frac{E_1}{C_1 h_1}$ while

N_2 approaches 0

Thus, if E_1/C_1 is greater than E_2/C_2, the second species continually decreases and the first species approaches $\frac{E_1}{C_1 h_1}$.

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